

REVISION OF NORTH AND CENTRAL AMERICAN NAJAS (NAJADACEAE)¹

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Najas is a cosmopolitan genus of submerged aquatic plants with its greatest diversity in tropical and subtropical regions. In North America, individuals of the genus can be separated from other aquatic genera by the plants of *Najas* possessing sub-opposite serrulate leaves and axillary imperfect flowers. Although floristic treatments have been prepared for certain areas—e.g., eastern United States (Clausen 1936) and Panama (Wentz and Haynes 1973)—at no time since Rendle (1901) have all the species, either worldwide or regional, been included in one revisionary treatment. Morphological variability within the group has been poorly understood. Because of the lack of a thorough revisionary treatment and a poor understanding of the taxa, the genus is, I believe, in need of revision.

The genus *Najas* has been divided into two subgenera, *Najas* and *Caulinia*, by Ascherson (1864) with *Najas* being dioecious and *Caulinia* being monoecious. Magnus (1889) separated subgenus *Caulinia* into two sections, *Americanae* with sloping leaf sheaths and *Euvaginatae* with truncate to auriculate leaf sheaths. Rendle (1899) divided the subgenus into two more sections, *Spathaceae* with staminate and carpellate flowers enclosed in floral envelopes and *Nudae* with no flowers enclosed in floral envelopes. According to Rendle (1899), the sections *Americanae* and *Euvaginatae* were composed of plants with staminate flowers enclosed in floral envelopes and carpellate flowers without such envelopes. Wilde (1961), in an investigation of Asiatic and Malaysian species of *Najas*, determined the presence of the envelopes to be too inconsistent to segregate sections. He thus proposed the abolition of Rendle's sections.

Variation in vegetative parts (plasticity) within individual taxa of aquatic plants has been recognized in *Callitriche* (Fassett 1951), *Halodule* (Phillips 1967), *Nymphaea* (Williams 1970), *Najas minor* (Wentz & Stuckey 1971), and *Potamogeton* (Haynes 1974). These workers concluded that because of this plasticity, the taxonomy of the genera in question should rest primarily on reproductive characters. As a result of my field work and the examination of several thousand herbarium specimens, I have found considerable plasticity within the leaf sheaths of *Najas*. I have concluded, therefore, that the separation of sections based upon the shape of the auricles is super-

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ficial. I agree with Wilde that four sections are unwarranted. Wilde (1961) also suggested that the two subgenera be reduced to sections because of the "great resemblance of *N. marina* to other species of *Najas* . . ." I agree that *N. marina* resembles the other species. However, with *N. marina* being dioecious, having a testa several cell layers thick, and having prickly internodes and dorsal surface of the laminae—the other species are monocious, have a testa three cell layers thick, and do not have prickly internodes and dorsal surfaces of the laminae—I believe the subgeneric category to be warranted.

The nomenclature of *Najas* is difficult. Many of the taxa in North and Central America were named by Sprengel (1825), Braun (1864), and Magnus (1870, 1894). The specimens examined by these workers were deposited at Berlin and later were destroyed during World War II. Gerloff (personal communication) informs me that no pre-World War II specimens of *Najas* (including the Willdenow collection) remain at Berlin. Therefore, I have had to resort to published descriptions and accepted usage of many names. In some instances (see Haynes and Wentz 1974) when only one or two taxa of *Najas* occur in an area, there is good evidence for my decision. In others, however, I have only the accepted usage and description to follow.

The morphology, systematic relationships, and economic value of *Najas* were discussed by Haynes (1977). Evidence from field work has indicated that *Najas* is just as morphologically plastic as *Callitriche* (Fassett 1951), *Potamogeton* (Haynes 1974), and *Ranunculus* (Bostrack and Millington 1962). Just as workers in these other genera have resorted to reproductive characters as a basis of a classification, I believe that a classification based mostly on reproductive structures is the only one workable for *Najas*. One should always attempt to collect specimens of *Najas* with seeds (Fig. 8). Just as identification of a sterile *Aster* may be nearly impossible, it is difficult at best to determine a sterile *Najas*.

The treatment that follows is based on field study and an examination of approximately 5000 herbarium specimens from 35 North American and European herbaria: A, ALU, AUA, B, BH, CAN, DAO, F, FSU, GA, GH, JEPS, K, KANU, KNK, LAF, LSUS, MEXU, MICH, MIN, MO, NCSC, NY, OS, PH, TENN, UC, UNA, UNC, UMBS, US, USF, UTC, VDB, and WIS (abbreviations according to Holmgren and Keuken 1974). Keys are based upon materials containing seeds; dimensions of leaves are taken from the fully expanded; longest leaves of a specimen; measurements of widths are taken approximately at the widest point of the leaf; and descriptions of the seeds are taken strictly from mature structures (Fig. 8).

NAJAS Linnaeus, Sp. Pl. 2: 1015. 1753; Gen. Pl. ed. 5. 445. 1754.

Caroliniana Raf., J. Phys. Chim. Hist. Nat. Arts 89:259. 1819.

Caulinia Willd., Mém. Acad. Roy. Sci. Hist. (Berlin) 87. 1798.

Fluvialis Adans., Fam. Pl. 2:472. 1763.

Hyas Dumort., Anal. Fam. Pl. 61. 1829.

Ittnera C. C. Gmel., Fl. Bad. 3:590. 1808.

Plants glabrous, herbaceous, annual or rarely perennial, aquatic, submersed in fresh or brackish waters, monoecious or dioecious. Stems slender, much branched, rooting at the lower nodes, sometimes armed with prickles on the internodes. Leaves subopposite or appearing whorled due to reduced internode length, sessile, each divided into lamina and sheath. Laminae linear and flattened, 1-nerved, sometimes dorsally armed with prickles on the midrib; margins usually serrulate with 5–100 teeth per side; apex acute to acuminate, with 1–3 teeth per side; teeth multicellular, formed by layers of cells decreasing in cell number outward terminated by a large, sharp-tipped cell, or unicellular. Sheaths variously shaped, each enclosing a pair of tiny hyaline scales; margins usually toothed with 1–15 teeth per side. Flowers imperfect, axillary, sessile or short pedunculate, solitary or clustered, often subtended by an involucre; involucre clear, bronze, brown, light green, purple, or red-purple. Staminate flowers subtended by a membranous involucre or the involucre rarely absent, each consisting of a single stamen; peduncle at first short, elongating at anthesis, pushing the anther through the involucre; anther sessile, 1- or 4-loculed, dehiscing irregularly; pollen 3-celled, globular or ellipsoid, densely filled with starch, monocolpate, the wall with shallow reticulations, thin, not divided into exine and entire. Carpellate flowers sessile, 1-loculed, 1-ovuled; involucre absent or rarely present; ovule basal, anatropous, with 2 integuments; gynoecial wall 2 cell layers thick, ending in a short style with 2–4 branches. Fruit 1-seeded, dehiscing by decay of gynoecial wall; gynoecial wall extremely delicate, closely enveloping the seed. Seeds without endosperm, areolate, with a basal raphe, fusiform to obovate, occasionally asymmetrical at apex or recurved; testa hard, brittle, 3 or several cell-layered, pitted or smooth; areolae formed by outer two layers of testa, variously rectangularly shaped, irregularly arranged or in 15–60 rows, the end walls often raised, giving the testa a papillose appearance; embryo elongate, without lateral enlargement of cotyledons. TYPE SPECIES: *N. marina* L. (From the Greek, *naias*, a water-nymph.)—Bushy-pondweed, Naiad, Water-Nymph.

KEY TO THE TAXA

1. Plants dioecious; testa pitted, 4 or more cell layers thick; internodes and dorsal surfaces of lamina with prickles; seeds 1.2 mm wide or wider 1. *N. marina*
1. Plants monoecious; testa smooth or pitted, 3 cell layers thick; internodes and dorsal surface of lamina without prickles; seeds 1.2 mm or less wide, *if* 1.2 mm wide, *then* with smooth testa 2
2. Seeds asymmetrical at apex or recurved 3
3. Areolae broader than long, ladder-like; teeth multicellular 7. *N. minor*
3. Areolae longer than broad, never ladder-like; teeth unicellular 4
4. Seeds strongly recurved; areolae in 10–20 rows; leaves in age stiff, recurved 6. *N. ancistrocarpa*
4. Seeds asymmetrical at apex but not recurved; areolae in 35–45 rows; leaves in age limp and spreading to ascending 5. *N. gracillima*
2. Seeds symmetrical at apex, not recurved 5

5. Lamina teeth unicellular, (18-) 30-100 per side 6
 6. Testa smooth, glossy; seeds obovate, brown to yellow; anthers 1-loculed 2. *N. flexilis*
 6. Testa pitted, dull; seeds fusiform, yellowish-white to greenish-brown; anthers 1- or 4-loculed 7
 7. Leaf sheaths deeply auriculate; restricted in North America to California 4. *N. graminea*
 7. Leaf sheaths rounded to truncate; widespread 8
 8. Seeds 3.3-3.8 mm long; areolae arranged in 50-60 rows 3d. *N. guadalupensis* var. *muenscheri*
 8. Seeds 2.5 mm or less long; areolae in fewer than 50 rows 9
 9. Teeth evident to unaided eye; anthers 1-loculed 3c. *N. guadalupensis* var. *floridana*
 9. Teeth invisible to unaided eye; anthers 4-loculed 10
 10. Laminae with 50-100 teeth per side; stems 0.8 mm or less in diameter 3a. *N. guadalupensis* var. *guadalupensis*
 10. Laminae with less than 50 teeth per side; stem 1.0 mm or more in diameter 3b. *N. guadalupensis* var. *olivacea*
 5. Lamina teeth multicellular, 5-25 per side 11
 11. Seeds 2 mm long or longer; areolae arranged in ca. 50 rows, elongate; teeth shorter than rest of the lamina is wide 9. *N. arguta*
 11. Seeds less than 2 mm long; areolae arranged in ca. 20 rows, 5-sided, all sides about equal; teeth longer than rest of lamina is wide 8. *N. wrightiana*

NAJAS subgenus NAJAS

Plants dioecious. Stem slender, much branched, rooting at the lower nodes, usually armed with prickles on the internodes. Leaves subopposite or appearing whorled, sessile; laminae coarsely serrate, the teeth multicellular, the midrib with prickles. Flowers solitary; anthers 4-loculed. Seeds 2.2-4.5 mm long; testa several (more than 3) cell layers thick; areolae arranged irregularly. Species 1. TYPE SPECIES: *N. marina* L.

1. NAJAS MARINA L., Sp. Pl. 2: 1015. 1753.

Ittnera major C. C. Gmel., Fl. Bad. 3:590. 1808.

I. najas C. C. Gmel., Fl. Bad. 3:590. 1808.

Najas gracilis Morong, Mem. Torrey Bot. Club 3(2):61. 1893.

N. gracilis Small, Fl. Southeastern U. S. 40. 1903.

N. latifolia A. Br., J. Bot. 2:276. 1864.

N. latior F. Muell. ex K. Schum. in Martius, Fl. Brasiliensis 3(3):804. 1894.

N. marina var. *angustifolia* (A. Br.) K. Schum. in Martius, Fl. Brasiliensis 3(3):725. 1894.

N. marina var. *angustissima* K. Schum. in Martius, Fl. Brasiliensis 3(3):725. 1894.

N. mariana var. *bollei* K. Schum. in Martius, Fl. Brasiliensis 3(3):726. 1894.

N. marina var. *brevifolia* Rendle, Trans. Linn. Soc. London, Bot. 5:396. 1899.

N. marina var. *californica* Rendle, Trans. Linn. Soc. London, Bot. 5:398. 1899.

N. marina var. *denticulata* Rendle, Trans. Linn. Soc. London, Bot. 5:438. 1900.

N. marina var. *ehrenbergii* (A. Br.) K. Schum. in Martius, Fl. Brasiliensis 3(3):276. 1894.

N. marina var. *genuina* K. Schum. in Martius, Fl. Brasiliensis 3(3):724. 1894.

N. marina var. *gracilis* (Morong) Dudley, Cornell Univ. Sci. Bull. 2:104. 1886.

- N. marina* var. *latifolia* (A. Br.) K. Schum. in Martius, Fl. Brasiliensis 3(3):725. 1894.
- N. marina* var. *latior* F. Muell. ex K. Schum. in Martius, Fl. Brasiliensis 3(3):725. 1894.
- N. marina* var. *mexicana* Rendle, Trans. Linn. Soc. London, Bot. 5:398. 1899.
- N. marina* var. *multidentata* (A. Br.) K. Schum. in Martius, Fl. Brasiliensis 3(3):726. 1894.
- N. marina* var. *muricata* (Raffeneau-Delile) K. Schum. in Martius, Fl. Brasiliensis 3(3):725. 1894.
- N. marina* var. *paucidentata* (A. Br.) K. Schum. in Martius, Fl. Brasiliensis 3(3):726. 1894.
- N. marina* var. *recurvata* Dudley, Cornell Univ. Sci. Bull. 2:104. 1886.
- N. major* All., Fl. Pedem. 2:221. 1785.
- N. major* var. *angustifolia* A. Br., J. Bot. 2:275. 1864.
- N. major* var. *ehrenbergii* A. Br., J. Bot. 2:275. 1864.
- N. major* var. *gracilis* Morong, Bot. Gaz. (Crawfordsville) 10:225. 1885.
- N. major* var. *intermedia* A. Br., J. Bot. 2:276. 1864.
- N. major* var. *microcarpa* A. Br., J. Bot. 2:276. 1864.
- N. major* var. *multidentata* A. Br., J. Bot. 2:275. 1864.
- N. major* var. *paucidentata* A. Br., J. Bot. 2:276. 1864.
- N. muricata* Raffeneau-Delile, Descr. Egypte, Hist. Nat. 281. 1813.

Plants dioecious. Stems 6–45 cm long, 0.5–4.0 mm in diameter, branched upward; internodes 0.3–11.0 cm long, with or without prickles. Leaves 0.5–3.9 cm long; laminae spreading to ascending, 0.4–4.5 mm wide, acute with 1 tooth at apex, coarsely serrate with 8–13 teeth per side, the terminal teeth similar in size and structure to the lateral teeth, the teeth multicellular, the midrib with prickles; sheaths 2.0–4.4 mm wide, wider than the laminae, acute, the teeth similar in size and structure to those of the laminae. Flowers solitary, the involucre brown to slightly purple; staminate flowers 1.7–3.0 mm long, the involucre beaks 0.3–0.7 mm long, 2-lobed, the anther 1.7–3.0 mm long, 4-loculed; carpellate flowers 2.5–5.7 mm long, the style 1.2–1.7 mm long, the stigma 3-lobed. Seeds 2.2–4.5 mm long, 1.2–2.2 mm wide, reddish brown, ovoid, the testa pitted, the areolae 3–4-angled, ca. 0.2 mm long, 0.1 mm broad, irregularly arranged, the end walls slightly raised (Fig. 8A). Chromosome number, $2n = 12$ (Viinikka 1973).

Brackish or highly alkaline waters of ponds and lakes, North and South Dakota to western New York; California to Utah, south to Panama; Florida and Caribbean islands (Fig. 1).

TYPE: Europe maribus (Holotype: LINN; Microfiche #1156 IDC 1945. 682:II 6, 7).

With its prickly internodes and prickles along the undersurface of the leaves, *N. marina* is the easiest of our *Najas* to recognize. The species is variable in the size of leaves, teeth, and seeds and, as a result, has been divided into numerous varieties. These differences usually can be found within single populations and, therefore, do not warrant taxonomic recognition. Viinikka (1973), however, observed two cytological races of the species, one race with B chromosomes and one without these accessory chro-

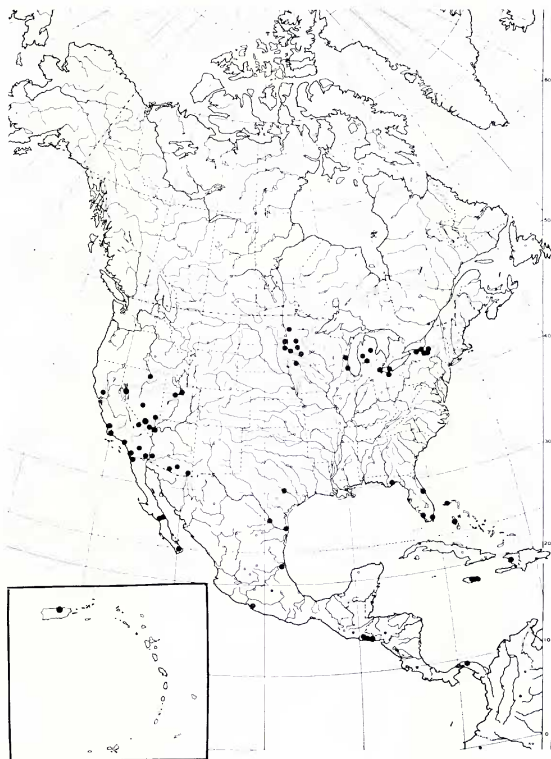


Fig. 1. Map of North America showing the documented distribution of *Najas marina*. (Caribbean islands inserted.)

mosomes. He examined one population from North America (Erie County, Ohio) and observed B chromosomes from those individuals (personal correspondence). He indicated (personal correspondence) that, in Europe, plants from the two races are morphologically different. Specimens with large seeds and leaves (no size given) invariably do not possess B chromosomes, whereas those with smaller seed and leaves do possess B chromosomes. He has not yet determined how to rank these apparent entities.

NAJAS subgenus CAULINIA (Willd.) Aschers., Fl. Prov. Brandenburg I:670. 1864.

Plant monoecious. Stem slender, much branched, rooting at the lower nodes, the internodes without prickles. Leaves subopposite or appearing whorled, sessile; laminae minutely serrulate to serrate, the teeth unicellular or multicellular, the midrib without prickles. Flowers solitary or clustered; anthers 1- or 4-loculed. Seeds 0.7-3.8 mm long; testa 3 cell layers thick; areolae arranged in longitudinal rows. Species 2-9. LECTOTYPE SPECIES: *Caulinia flexilis* Willd. = *N. flexilis* (Willd.) Rostk. & Schmidt. (Lectotype here designated.)

2. NAJAS FLEXILIS (Willd.) Rostk. & Schmidt, Fl. Sedin. 382. 1824.

Caulinia flexilis Willd., Mem. Acad. Roy. Sci. Hist. (Berlin) 95. 1798.

Flurialis flexilis (Willd.) Pers., Synops. 2:530. 1807.

Najas canadensis Michx., Fl. Bor. Amer. 2:220. 1803.

N. caespitosus (Maguire) Reveal in Welsh, Atwood, & Reveal, Great Basin Naturalist 35:357. 1976.

N. flexilis subsp. *caespitosa* Maguire & Jensen, Rhodora 44:7. 1942.

N. flexilis var. *congesta* Farwell, Rep. Michigan Acad. Sci. 21:348. 1920.

N. flexilis var. *robusta* Morong, Bot. Gaz. (Crawfordsville) 10:255. 1885.

Plants monoecious. Stems 2.5-50 cm long, 0.2-0.6 mm in diameter, often profusely branched above; internodes 0.16-6.8 cm long, without prickles. Leaves 0.8-4.2 cm long; laminae spreading to ascending, 0.2-0.6 mm wide, acute with 1-2 teeth at apex, minutely serrulate with 35-80 teeth per side, the terminal teeth similar in size and structure to the lateral teeth, the teeth unicellular, the midrib without prickles; sheaths 0.7-1.6 mm wide, wider than the laminae, round, minutely serrulate with 8-10 teeth per side, the teeth similar in size and structure to those of the laminae. Flowers 1 (-2) per axil, the staminate in the upper axils, the carpellate throughout, the involucre bronze; staminate flowers 1.1-2.7 mm long, the involucre beaks 0.7-1.2 mm long, 3-lobed, the anthers 1.1-2.7 mm long, 1-loculed; carpellate flowers 2.5-4.7 mm long, the style 1.5-1.7 mm long, the stigma 3-lobed. Seeds (1.2-) 2.5-3.7 mm long, 0.2-1.2 mm wide, deep brown to yellow, narrowly to broadly obovate, the testa smooth, the areolae 5-6-angled, ca. 0.2 mm long, ca. 0.1 mm wide, in ca. 50 rows, without raised end walls (Fig. 8B). Chromosome number unknown.

Lakes and rivers, Nebraska, Missouri, and Maryland, north to southwestern

Ontario and Newfoundland; Alberta and Saskatchewan south to western Oregon and central Utah (Fig. 2).

TYPE: Pennsylvania (Holotype: B; microfiche # 17094 IDC 7440. 1224; III. 2.)

In habit, *N. flexilis* is most similar to *N. guadalupensis*. However, when seeds are present, *N. flexilis* can be easily separated from the latter species by the glossy, smooth, yellowish seeds that are widest above the middle.

Several different varieties have been proposed for North American individuals of *N. flexilis*, e.g., var. *robusta* Morong, var. *congesta* Farwell, and var. *caespitosa* Maguire and Jensen. These varieties are based, for the most part, on differences in vegetative structures. Clausen (1936), in discussing some of these different forms, stated "Different forms of the species do occur, but the characters, such as width of leaves, size and shape of seeds, and habit, occur in all sorts of combinations and can not be correlated with geographical areas to give definite geographical races or varieties which are worth naming." I have reached the same conclusion.

Najas flexilis is probably the most common *Najas* in the northern United States. Wentz and Stuckey (1971), however, indicated that the species is becoming less common in Ohio. This decrease in abundance apparently corresponds with the increase in turbidity and general decline in water quality of natural lakes and rivers.

3. NAJAS GUADALUPENSIS (Sprengel) Magnus, Beitr. Gatt. *Najas* 8. 1870.

Plants monoecious. Stems 11.0–90.0 cm long, 0.1–2.0 mm in diameter, profusely branched; internodes 0.1–9.0 cm long, without prickles. Leaves 0.3–3.3 cm long; laminae spreading, 0.2–2.1 mm wide, round obtuse to acuminate with 1–3 teeth at apex, minutely serrulate with 18–100 teeth per side, the terminal tooth slightly larger than but similar in structure to the lateral teeth, the teeth unicellular, the midrib without prickles; sheaths 1.0–3.4 mm wide, wider than the laminae, round to slightly auriculate, serrulate with 4–8 teeth per side, the teeth similar in size and structure to those of the laminae. Flowers 1–3 per axil, the staminate in the upper axils, the carpellate in the lower axils, the involucre purple-tinged; staminate flowers 1.5–3.0 mm long, the involucre beaks 0.2–1.3 mm long, 4-lobed, the anther 1.0–1.7 mm long, 1- or 4-loculed; carpellate flowers 1.5–4.0 mm long, the styles 0.3–1.5 mm long, the stigmas 4-lobed. Seeds 1.2–3.8 mm long, 0.4–0.8 mm wide, purple-tinged, fusiform, the testa pitted, the areolae 4–6-angled, 0.08–0.1 mm long, ca. 0.08 mm wide, in 20–60 rows, the end walls not raised. Chromosome number, $2n = 12, 36, 42, 48, 54, 60$ (Chase 1947 a,b).

Najas guadalupensis has long been considered a highly variable species (Fernald 1923). Clausen (1936), Ooststroom (1939), Wentz and Haynes (1973), and Haynes and Wentz (1974) discussed variability within the species and suggested that the complex should possibly be considered as

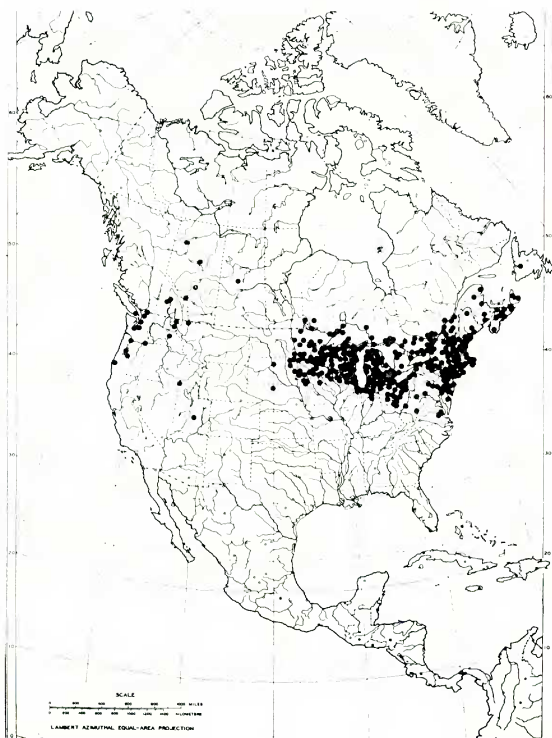


Fig. 2. Map of North America showing the documented distribution of *Najas flexilis*.

several closely related taxa. Rosendahl and Butters (1935) named *N. olivacea*. It was said to differ from *N. guadalupensis* in its stouter habit, its larger seeds, and its testa. Clausen (1937) separated *N. muenscheri* from *N. guadalupensis* by its more slender habit and its seeds with smaller areolae.

From my field work and the examination of thousands of specimens of *N. guadalupensis* and most of these available of *N. muenscheri* and *N. olivacea*, I have concluded that *N. olivacea* and *N. muenscheri* represent populations of *N. guadalupensis* at the northern limit of its range. They are slightly different from most individuals of *N. guadalupensis*. However, intermediates do exist. Thus, I think they should be recognized but do not believe that specific rank is justified. I consider varieties as morphogeographic subdivisions of a species that presumably reflect genetic differences (Kapadia 1963). I have therefore chosen to recognize the taxa that have been called *N. olivacea* and *N. muenscheri* as varieties of *N. guadalupensis*.

By having unicellular teeth on the margin of the lamina, *N. guadalupensis* resembles *N. flexilis* and *N. graminea*. The seeds of *N. guadalupensis* are pitted; those of *N. flexilis* are smooth. The sheaths of *N. guadalupensis* are rounded to slightly auriculate; those of *N. graminea* are deeply auriculate.

3a. NAJAS GUADALUPENSIS var. GUADALUPENSIS

Caulinia guadalupensis Sprengel, Syst. Vegetabilium 1:20. 1824.

Najas flexilis var. *curassavica* A. Br., J. Bot. 2:277. 1864.

N. flexilis var. *fusiformis* Chapman, Fl. Southern U. S. 444. 1883.

N. flexilis var. *guadalupensis* (Sprengel) A. Br., J. Bot. 2:276. 1864.

N. microdon var. *curassavica* A. Br., Sitzb. Ges. Naturf. Fr. Berlin. 1868.

N. microdon var. *guadalupensis* (Sprengel) A. Br., J. Bot. 2:276. 1864.

N. urbaniana O. C. Schmidt, Fedde Rep. Spec. Nov. 22:99. 1925.

Stems 11–75 cm long, 0.1–0.8 mm in diameter. Leaves 0.3–2.8 mm long; laminae 0.2–1.8 mm wide, acute to mucronate, with 50–100 teeth per side; sheaths 1.0–1.9 mm wide, round, with 5–8 teeth per side. Flowers 1–3 per axil; staminate 1.5–2.5 mm long, the involucre beak 0.2–0.6 mm long, the anther elliptic, 4-loculed; carpellate flowers 1.5–2.0 mm long. Seeds 1.2–2.5 mm long, 0.4–0.6 mm wide, the areolae in ca. 20 rows (Fig. 8C).

Lakes, rivers, and canals, southern Maine to southern Alberta and Washington, south to Guadalupe, Curacao, and Panama (Fig. 3).

TYPE: Guadeloupe (B, destroyed during World War II).

3b. NAJAS GUADALUPENSIS var. olivacea (Rosendahl & Butters) Haynes, comb. & stat. nov.

Najas olivacea Rosendahl & Butters, Rhodora 37:347. 1935.

Stems 15–40 cm long, 1.0–2.0 mm in diameter. Leaves 0.9–1.8 cm long; laminae 1.5–2.0 mm wide, acute, with 20–40 teeth per side; sheaths 2.5–3.4 mm wide, round to slightly auriculate, with 4–8 teeth per side. Flowers 1 per axil; staminate flowers 2.3–2.8 mm long, the anther ovoid, 4-loculed; carpellate flowers 2.7–3.1 mm long. Seeds 2.3–2.5 mm long, 0.6–0.8 mm

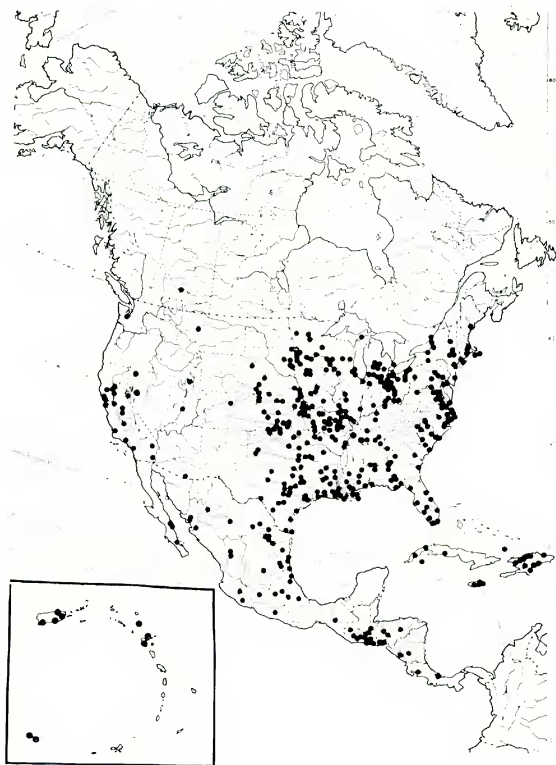


Fig. 3. Map of North America showing the documented distribution of *Najas guadalupensis* var. *guadalupensis*. (Caribbean islands inserted.)

wide, the areolae in 20–40 rows (Fig. 8D).

Lakes and rivers, Iowa to Manitoba, east to New York and Quebec (Fig. 4).

TYPE: UNITED STATES: MINNESOTA: Kandiyohi Co.: growing in tufts in 1–3 feet of water, muddy bottoms; abundant in NE bay of Norway Lake, 6 Sep 1933, *C. O. Rosendahl and F. K. Butters 6446* (Lectotype, MIN!; isotype, MIN!). (Lectotype here designated.)

3c. *NAJAS GUADALUPENSIS* var. *FLORIDANA* Haynes & Wentz, *Sida* 5:262. 1974.

Stems 7–51 cm long, 0.1–1.7 mm in diameter. Leaves 0.9–3.3 cm long; laminae 0.5–2.1 mm wide, round obtuse to acuminate, with 18–42 teeth per side; sheaths 1.2–2.5 mm wide, round, with 5–8 teeth per side. Flowers 1 per axil; staminate flowers 1.5–2.4 mm long, the anther elliptic, 1-loculed; carpellate flowers 1.0–3.5 mm long. Seeds 1.6–2.2 mm long, 0.3–0.8 mm wide, the areolae in ca. 20 rows (Fig. 8E).

In lakes, streams, and canals, Florida, central Alabama, and central Georgia (Fig. 4).

TYPE: UNITED STATES: FLORIDA: Dade Co.: abundant in brackish water of ditch along St. Rt. 41 at edge of Everglades National Park, ca. 40 mi. W of Miami, 5 Apr 1972, *W. A. Wentz 670* (Holotype, US!; isotypes, GH!, MICH!, OS!).

3d. *NAJAS GUADALUPENSIS* var. *muenscherei* (Clausen) Haynes, comb. & stat. nov.

Najas muenscherei Clausen, *Rhodora* 39:59. 1937.

Stems 30–90 cm long, 0.8–1.0 mm in diameter. Leaves 0.9–1.3 cm long; laminae 0.5–1.6 mm wide, acute, with 50–100 teeth per side; sheaths 1.0–1.5 mm wide, round, with 4–8 teeth per side. Flowers 1 per axil; staminate flowers 2.0–3.0 mm long, the anther elliptic, 1-loculed; carpellate flowers 2.9–4.0 mm long. Seeds 3.3–3.8 mm long, 0.5–0.7 mm wide, the areolae in 50–60 rows (Fig. 8F).

Shallow water of the Hudson River, New York (Fig. 4).

TYPE: UNITED STATES: NEW YORK: Greene Co.: Tidal mudflats of Hudson River, Imbocht Bay, 3 Sep 1936, *W. C. Muenschler and O. F. Curtis, Jr. 5495* (Holotype, BH!; isotype, GH!).

4. *NAJAS GRAMINEA* Raffeneau-Delile, *Descr. Egypte, Hist. Nat.* 281. 1813.

Caulina alagensis Pollini, *Hort. & Prov. Veron.* 26. 1816.

Najas alagensis (Pollini) Pollini, *Fl. Veron.* 3:49. 1824.

N. seminuda Griff. in Voigt, *Hort. Suburb. Calc.* 694. 1845.

Plants monoecious. Stems to 35 cm long, 0.2–0.5 mm in diameter, sparingly branched; internodes 0.4–1.9 cm long, without prickles. Leaves 0.8–2.0 cm long; laminae spreading to ascending, 0.5–1.0 mm wide, acute with 2–3

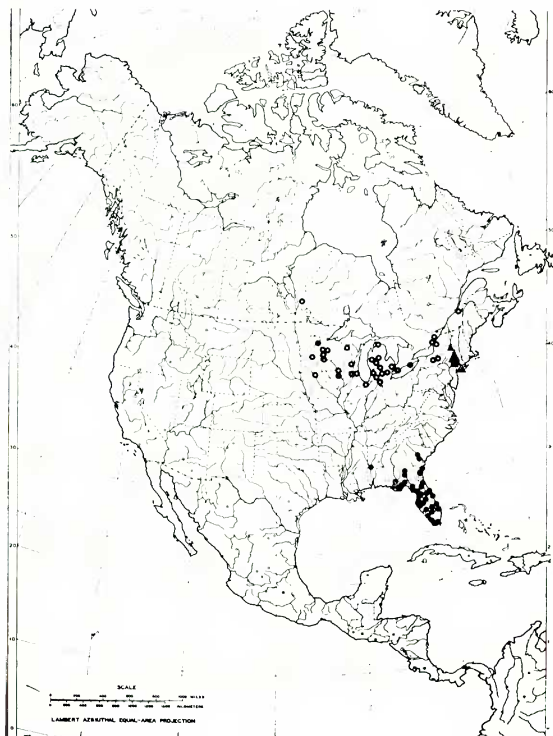


Fig. 4. Map of North America showing the documented distribution of *Najas guadalupensis* var. *floridana* (solid dots), *N. guadalupensis* var. *muenscheri* (solid triangles), and *N. guadalupensis* var. *olivacea* (dots with open star).

teeth at apex, minutely serrulate with ca. 40 teeth per side, the terminal teeth similar in size and structure to lateral teeth, the teeth unicellular, the midrib without prickles; sheaths 1.0–1.5 mm wide, wider than the laminae, deeply auriculate, minutely serrulate with 8–15 teeth per side, the teeth similar in structure and size to those of the laminae. Flowers 1–2 per axil, the staminate in the upper axils, the carpellate throughout, the involucre clear in color; staminate flowers 2.0–3.0 mm long, the involucre beaks 1.0–1.5 mm long, 4-lobed, the anther 1.5 mm long, 4-loculed; carpellate flowers to 3.5 mm long, the styles to 1.0 mm long, the stigmas 2-lobed. Seeds 1.7–2.5 mm long, 0.4–0.6 mm wide, greenish-brown, fusiform, the testa pitted, the areolae 4-angled, less than 0.1 mm long, less than 0.1 mm broad, in ca. 35 rows, the end walls slightly raised (Fig. 8G). Chromosome number, $2n = 48$ (Sharma and Chatterjee 1967).

Rice fields, California (Fig. 5).

TYPE: Egypt (MPU).

By the deeply auriculate sheaths, *N. graminea* is one of the easiest of the North and Central American *Najas* to recognize. A native of southeast Asia, the species apparently was introduced into California prior to 1946 and now is evidently quite rare there. I have seen no recent specimens of the species from North or Central America.

Rendle (1901) placed this species in the section *Nudae* based upon the lack of any floral involucre. Wilde (1961), however, demonstrated the presence of a leaf-like involucre and used this as evidence to abolish the section.

5. *NAJAS GRACILLIMA* (A. Br. ex Engelm. in A. Gray) Magnus, Beitr. Gatt. *Najas* 23. 1870.

Najas indica (Willd.) Cham. var. *gracillima* A. Br. ex Engelm. in A. Gray, Man. Bot. (ed. 5) 681. 1868.

Plants monoecious. Stems 4.5–48 cm long, 0.2–0.7 mm in diameter, slightly branched; internodes 0.1–3.2 cm long, without prickles. Leaves 0.6–2.8 cm long; laminae spreading to ascending, 0.1–0.5 mm wide, acute with 2–3 teeth at apex, minutely serrulate with 13–17 teeth per side, the terminal teeth similar in size and structure to the lateral teeth, the teeth unicellular, the midrib without prickles; sheaths 0.5–1.5 mm wide, wider than the laminae, truncate, minutely serrulate with 7–8 teeth per side, the teeth similar in size and structure to those of the laminae. Flowers 1–3 per axil, the staminate in the upper axils, the carpellate throughout, the involucre bronze to purple; staminate flowers 1.5–2.0 mm long, the involucre beaks ca. 0.8 mm long, 2-lobed, the anther ca. 1.3 mm long, 1-loculed; carpellate flowers 0.5–2.7 mm long, the styles 0.3–1.5 mm long, the stigmas 2-lobed. Seeds 2.0–3.2 mm long, 0.4–0.7 mm wide, light brown, fusiform with the style arising from one side at the apex, the testa pitted, the areolae 4-angled, less than 0.1 mm long, less than 0.1 mm wide, in ca. 40 longitudinal rows,

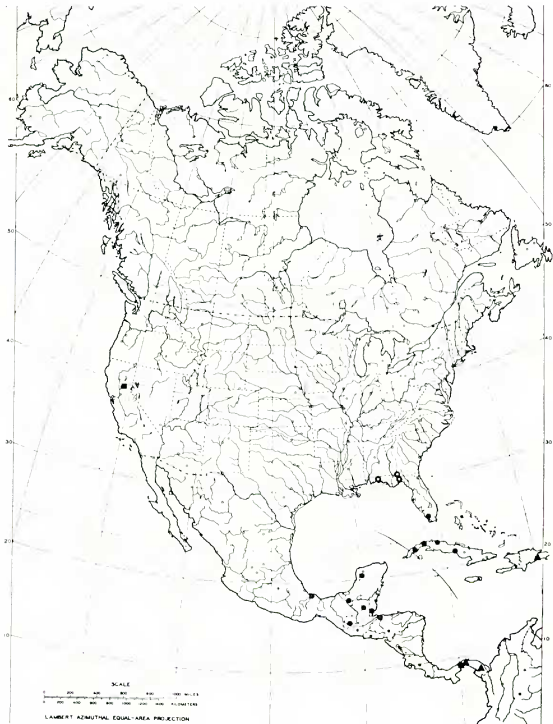


Fig. 5. Map of North America showing the documented distribution of *Najas graminea* (solid square), *N. ancistrocarpa* (dots with open star), *N. arguta* (solid triangles), and *N. wrightiana* (solid dots).

the end walls raised (Fig. 8H). Chromosome number unknown.

In soft water lakes, Nova Scotia to Alabama, west to Minnesota and Missouri; California (Fig. 6).

TYPE: Northeast United States (B, destroyed during World War II).

Najas gracillima is most similar to *N. minor*, especially in vegetative condition (see discussion under *N. minor*). *Najas gracillima*, however, can be separated from the latter species by its style arising off-center at the apex of the gynecial wall and by its areolae being longer than broad.

The species, once more common than it is now (Wentz and Stuckey 1971), apparently cannot tolerate pollution and has become exceedingly rare due to the gradual degradation of lakes and streams in eastern United States.

6. NAJAS ANCISTROCARPA Magnus, Beitr. Gatt. *Najas* 7. 1870.

Plants monoecious. Stems 7–22 cm long, 0.2–1.0 mm in diameter, profusely branched; internodes 0.2–4.0 cm long, without prickles. Leaves 0.8–2.6 cm long; laminae usually recurved with age, 0.1–0.7 mm wide, acute with 1 tooth at apex, conspicuously serrulate with 5–9 teeth per side, the terminal tooth slightly larger than but similar in structure to the lateral teeth, the teeth multicellular, the midrib without prickles; sheaths 1.0–1.3 mm wide, wider than the laminae, round to slightly auriculate, serrulate with 3–5 teeth per side, the teeth similar in structure and size to those of the laminae. Flowers 1 per axil, the staminate in the upper axils, the carpellate in the lower axils, the involucre bronze colored; staminate flowers 2.0–3.0 mm long, the involucre beaks ca. 0.4–0.6 mm long, 4-lobed, the anther 1.5–2.0 mm long, 4-lobed; carpellate flowers to 2.5 mm long, the styles less than 0.4 mm long, the stigmas 4-lobed. Seeds 2.5–3.0 mm long, 0.5–0.7 mm wide, greenish-brown, recurved, the testa pitted, the areolae 4-angled, to 0.2 mm long, ca. 0.05 mm broad, in ca. 20 longitudinal rows, the end walls raised (Fig. 8I). Chromosome number unknown.

In lakes, southern Georgia and northern Florida (Fig. 5).

TYPE: JAPAN: *Yokohama* (B, destroyed during World War II).

Najas ancistrocarpa, according to Rendle (1901) and Miki (1935), is exceedingly rare and has been known only from three Japanese islands, Honshiu, Shikoku, and Yokohama. The species is either not as restricted as it was once thought to be or it is spreading. Yang (1974) reported it new to Taiwan, and Haynes and Wentz (1974) recorded it for North America.

The species is known from four localities in North America: Open Pond and Cane Water Pond in Decatur County, Georgia; Milton in Santa Rosa County, Florida; and Lake Jackson in Leon County, Florida. This species is another of the many found in southeastern United States and southeastern Asia (Graham 1972).

The vegetative organs of *N. ancistrocarpa* resemble those of *N. minor* and *N. wrightiana* by the presence of large teeth scattered along the margin of

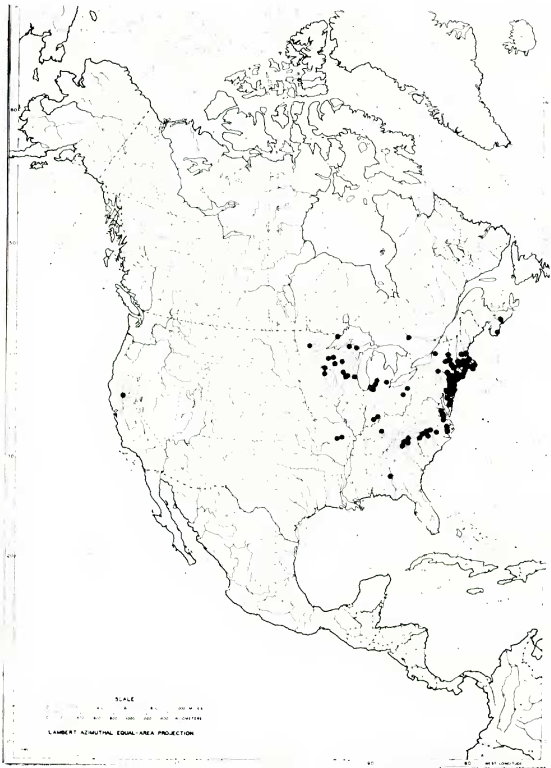


Fig. 6. Map of North America showing the documented distribution of *Najas gracillima*.

quite narrow leaves. However, *N. ancistrocarpa* is easily distinguished from the latter two species by its recurved fruits (sometimes crescent-shaped). I know of no other *Najas* with such curved fruits.

7. *NAJAS MINOR* Allioni, Fl. Pedemon. 2:221.1785.

Caulinia fragilis Willd., Mem. Acad. Roy. Sci. Hist. (Berlin) 94. 1798.

C. indica. Willd., Mem. Acad. Roy. Sci. Hist. (Berlin) 95. 1798.

C. minor (Allioni) Coss & Germ., Fl. Paris 575. 1845.

Fluvialis minor (Allinoti) Pers., Synops. 2:530. 1807.

Ittnera minor (Allioni) C. C. Gmel., Fl. Bad. 3:590. 1808.

Najas australis Bory ex Cham., Linnæa 4:501. 1829.

N. dichotoma Roxb., Hort. Beng. 71. 1814.

N. fragilis (Willd.) Rostk. & Schmidt, Fl. Sedin. 382. 1824.

N. indica (Willd.) Cham., Linnæa 4:501. 1829.

N. minor var. *setacea* A. Br., J. Bot. 2:278. 1864.

N. setacea (A. Br.) Rendle, Trans. Linn. Soc. London, Bot. 5:422. 1899.

N. subulata Thuill., Fl. Paris (ed. 2) 500. 1800.

N. ternata Roxb. ex. Gric., Notul. 3:183. 1851.

Plants monoecious. Stems 11–120 cm long, 0.2–1.0 mm in diameter, profusely branched near apex; internodes 0.5–5.8 cm long, without prickles. Leaves 0.5–3.4 cm long; laminae usually recurved with age, 0.1–1.2 mm wide, acute with 1–2 teeth at apex, conspicuously serrulate with 7–15 teeth per side, the terminal teeth similar in size and structure to the lateral teeth, the teeth multicellular, the midrib without prickles; sheaths 1.0–3.0 mm wide, wider than the laminae, truncate to auriculate, serrulate to lacerate with 5 to 8 teeth per side, the teeth similar in size and structure to those of the laminae. Flowers 1–2 per axil, the staminate in the upper axils, the carpellate throughout, the involucre light green to purple; staminate flowers 1.9–2.2 mm long, the involucre beaks 0.4–2.1 mm long, 2-lobed, the anther ca. 0.3 mm long, 1-loculed; carpellate flowers ca. 2.2 mm long, the styles 1.0–1.2 mm long, the stigmas 2-lobed. Seeds 1.5–3.0 mm long, 0.5–0.7 mm wide, purplish, slightly recurved, the testa pitted, the areolae 4-angled, ca. 0.01 mm long, ca. 0.03 mm wide in ca. 15 longitudinal rows, the end walls not raised (Fig. 8J). Chromosome number, $2n = 12$ (Sharma and Chatterjee 1967).

Ponds, lakes, and slow moving streams; New York to Illinois, south to Florida, Mississippi, and Arkansas (Fig. 7).

TYPE: ITALY: Pedemont (Holotype, TO, photo, UNA!).

Najas minor, native of the Eastern Hemisphere, apparently invaded North America nearly 50 years ago (Meriläinen 1968, Wentz and Stuckey 1971). With the gradual eutrophication of the waters of eastern United States, the species has become quite widespread and, in fact, has become the most abundant *Najas* in some areas (Wentz and Stuckey 1971).

Najas minor, with its mature leaves recurved and with its areolae broader than long and arranged in longitudinal rows like the rungs of a ladder, is one of the more distinctive species of *Najas*. However, young sterile indi-

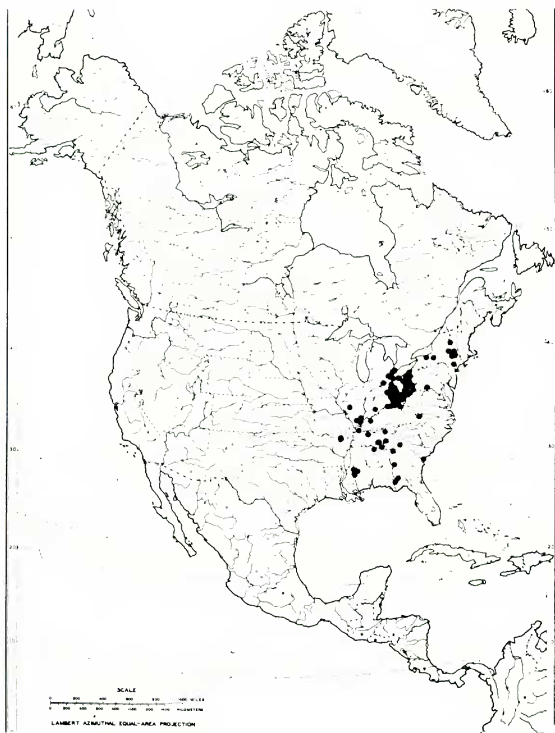
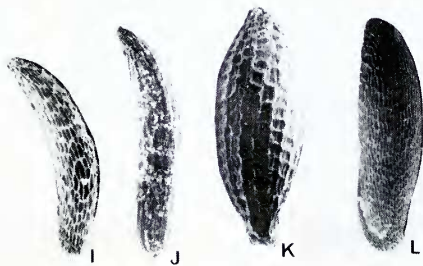
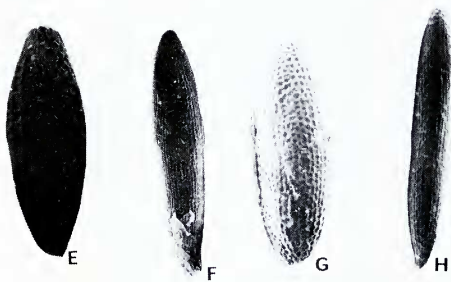
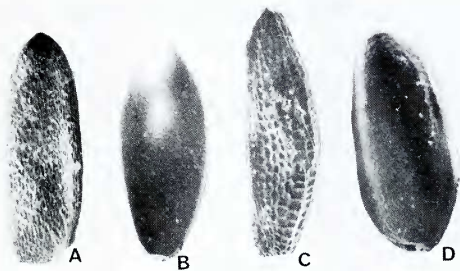


Fig. 7. Map of North America showing the documented distribution of *Najas minor*.

Fig. 8. *Najas* seeds. SEM micrographs taken at 20 KV. A. *N. marina* (X 9½). B. *N. flexilis* (X 18). C. *N. guadalupensis* var. *guadalupensis* (X 28¼). D. *N. guadalupensis* var. *olivacea* (X 25½). E. *N. guadalupensis* var. *floridana* (X 33½). F. *N. guadalupensis* var. *muenscheri* (X 19). G. *N. graminea* (X 23½). H. *N. gracillima* (X 19). I. *N. ancistrocarpa* (X 20¼). J. *N. minor* (X 19¼). K. *N. wrightiana* (X 43). L. *N. arguta* (X 18½).



viduals resemble *N. gracillima*. Meriläinen (1968) indicated that *N. minor* can be separated from the latter species by the former having recurved leaves and the latter having leaves not recurved. Wentz and Stuckey (1971) demonstrated that the leaves of *N. minor* do not become recurved until late in the growing season. Therefore, during the early growing season, individuals of *N. minor* could be mistaken for *N. gracillima* when one utilizes vegetative characters only.

8. *NAJAS WRIGHTIANA* A. Br., Sitzber. Ges. Naturf. Fr. Berlin 17. 1868.

Najas multidentata Koch, Ber. Schweiz. Bot. Ges. 44:341. 1935.

N. wrightiana subsp. *multidentata* (Koch) Clausen, Bull. Torrey Bot. Club 73:365. 1946.

Plants monoecious. Stems 9–45 cm long, 0.3–1.0 mm in diameter, profusely branched; internodes 0.3–5.2 cm long, without prickles. Leaves 0.5–2.6 cm long; laminae ascending, 0.2–1.3 mm wide, acute with 1 tooth at apex, conspicuously serrulate with 8–22 teeth per side, the terminal tooth similar in size and structure to the lateral teeth, the teeth multicellular, the midrib without prickles; sheaths 0.7–2.8 mm wide, wider than the laminae, round, serrulate with (1–) 3–5 teeth per side, the teeth similar in structure and size to those of the laminae. Flowers 1–2 per axil, the staminate in the upper axils, the carpellate in the lower axils, the involucre brown to red purple; staminate flowers 1.2–1.9 mm long, the involucre beaks 0.3–0.5 mm long, 2-lobed, the anther ca. 1.0 mm long, 4-loculed; carpellate flowers ca. 2.0 mm long, the styles to 0.7 mm long, the stigmas 4-lobed. Seeds 0.7–1.5 mm long, 0.3–0.5 mm wide, whitish, fusiform, the testa pitted, the areolae 5-angled, ca. 0.1 mm long, less than 0.1 wide, in ca. 20 longitudinal rows, the end walls raised (Fig. 8K). Chromosome number unknown.

Slow moving streams and ponds, Veracruz to Florida, south to Guatemala, Honduras, and Cuba (Fig. 5).

TYPE: CUBA (B, destroyed during World War II).

Najas wrightiana superficially resembles *N. arguta*. Clausen (1946) discussed this similarity and suggested that the two species could be separated by teeth of *N. wrightiana* being longer than the rest of the lamina is wide, whereas those of *N. arguta* are shorter than the rest of the lamina is wide. I believe, however, the best characters are those of the seed. The seeds of *N. wrightiana* are short (1.0–1.5 mm long) and have 5-angled areolae arranged in ca. 20 rows. *Najas arguta* seeds, on the other hand, are 2.1–2.6 mm long and have elongate areolae arranged in ca. 50 rows.

9. *NAJAS ARGUTA* H.B.K., Nov. Gen. et Sp. Pl. 1:371. 1815.

Caulinia tenella C. G. Nees in Neuwied, Reise Bras. 2:345. 1824.

Najas tenera Schrad., Gott. Gel. Anz. 2:715. 1825.

Plants monoecious. Stems 15–70 cm long, 0.3–1.0 mm in diameter, profusely branched; internodes 0.5–13.5 cm long, without prickles. Leaves 1.2–2.8

cm long; laminae spreading, 0.6–1.9 mm wide, acute to acuminate with 1 tooth at apex, conspicuously serrulate with 15–25 teeth per side, the terminal tooth slightly larger than but similar in structure to the lateral teeth, the teeth multicellular, the midrib without prickles; sheaths 1.2–3.4 mm wide, wider than the laminae, round to truncate, serrulate with 2–7 teeth per side, the teeth smaller than but similar in structure to those of the laminae. Flowers 1 per axil, the staminate in the upper axils, the carpellate in the lower axils, the involucre purple-tinged; staminate flowers 2.0–2.2 mm long, the involucre beaks ca. 0.5 mm long, 4-lobed, the anther to 1.6 mm long, 1-loculed; carpellate flowers 1.7–2.1 mm long, the styles ca. 0.5 mm long, the stigmas 3–4-lobed. Seeds 2.1–2.6 mm long, 0.6–0.8 mm wide, yellowish-white, elongate-fusiform, the testa pitted, the areolae sometimes inconspicuous, 5–6-angled, to 0.2 mm long, ca. 0.05 mm broad, in ca. 50 longitudinal rows, the end walls raised (Fig. 8L). Chromosome number unknown.

In lakes, Panama and the Dominican Republic (Fig. 5).

TYPE: Provenit in aquis prope momprox- Regno novogranatensi (P?).

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